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POPULATION CHARACTERISTICS OF THE RED PORGY, *PAGRUS PAGRUS*, STOCK OFF THE CAROLINAS

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ABSTRACT

Using recorded and estimated landings and size frequencies of fish from commercial, headboat, private recreational and charter boat fisheries from 1972-1986, we examined the age structure and population size of the stock of red porgy, *Pagrus pagrus*, off the coast of North and South Carolina. Combining annual age-length keys with length-frequency distributions, annual landings in numbers at age are estimated. Virtual population analysis (VPA) is applied to these data to estimate annual, age-specific population sizes and fishing mortality rates for three levels of natural mortality ($M = 0.20, 0.28, \text{ and } 0.35$). On average 3% to 6% of the population (ages 1 and older) was landed annually from 1972-1978 compared to 16% to 23% from 1982-1986. Eleven to 21% of fully recruited red porgy (ages 5 and older) were landed annually from 1972-1978 compared to 40% to 50% from 1982-1986. For the intermediate level of natural mortality ($M = 0.28$), estimated population size in biomass declined from 2.6 million kg in 1978 to 0.6 million kg in 1986. Spawning stock (ages 2-10) in biomass ranged between 0.5 million kg in 1986 and 1.5 million kg in 1977. Recruitment to age 1 in numbers ranged from 0.6 million in 1986 (from the 1985 spawning stock) to 2.2 million in 1973 (from the 1972 spawning stocks, respectively). For the low exploitation period (1972-1978), spawning stock biomass declined to 69% to 86% of unexploited spawning stock ($F = 0$); while for the high exploitation period (1982-1986), spawning stock biomass declined to 38% to 53% of unexploited spawning stock. Between these two exploitation regimes, spawning stock biomass for the high exploitation period was reduced to 55% to 62% of the spawning stock biomass for the earlier low exploitation period. Yield per recruit based on age-specific fishing mortality rates increased by about 53% from 121.1 g for the low exploitation period to 184.8 g for the high exploitation period. Because age-specific fishing mortality rates (F_i , ages 1-9) increased by a factor of 3.7, most of the gains available by increasing F have been taken. With proportionately greater increases in F_i incurred by younger age classes (ages 1-4) between 1972-1978 and 1982-1986, small gains in yield per recruit may now be obtained by raising age-at-entry to the fishery above the current age-1.

In this paper we compute and document changes in age structure and population size of red porgy, *Pagrus pagrus*, in the Atlantic Ocean off North Carolina and South Carolina. Red porgy, also known as silver snapper and pink snapper, is the most abundant reef fish after black sea bass, *Centropristis striata*, in headboat catches off North Carolina and South Carolina (Huntsman, 1976), has had increasing commercial importance and value, and is apparently one of the most abundant, larger (to 8 kg) species in the live bottom ecosystem of the southern U.S. Atlantic coast (Struhsaker, 1969). The red porgy is a reef-associated, demersal species commonly found over very irregular and low profile hard bottom at depths ranging from 18 to 183 m (Manooch and Hassler, 1978). Red porgy occur off the southern U.S. Atlantic coast, in the Gulf of Mexico, in the Atlantic off South America from Brazil to Argentina, off Portugal and Spain, in the Mediterranean Sea, off Africa south to the Cape Verde Islands, and around the Azores, Madeira, and Canary Islands. The red porgy is an esteemed food and game fish, and is taken by hook-and-line, trawls, and traps.

We assume the population of red porgy off North Carolina and South Carolina to be a single stock. Depending on the context, that assumption is relatively defensible. With respect to adult populations, the assumption is strong. Tagging

Table 1. Estimates of headboat (HB), charter boat (CB) and private boat (PB) landings of red porgy from North and South Carolina, mean weight from headboat survey, and landings in numbers

Year	Landings in biomass (10^3 kg)				Mean weight (kg)	Landings in numbers (10^3)
	HB	CB*	PB†	Total		
1972	235.35	17.27	0	252.62	1.09	231.81
1973	334.13	17.27	0	351.40	1.13	310.28
1974	233.39	17.27	0	250.66	0.99	251.96
1975	202.54	17.27	0	219.81	0.91	241.95
1976	178.64	17.27	0	195.91	0.91	216.38
1977	231.69	17.27	0	248.96	1.06	235.23
1978	205.64	17.27	0	222.91	1.17	191.22
1979	140.46	17.27	24.80	182.53	1.09	154.82
1980	149.56	17.27	10.39	177.23	1.01	174.51
1981	137.19	17.27	14.03	168.49	0.88	191.74
1982	189.52	17.27	14.03	220.81	0.71	305.71
1983	116.66	17.27	14.03	147.96	0.76	191.87
1984	95.11	17.27	4.31	116.69	0.77	152.05
1985	113.78	17.27	23.72	154.77	0.68	239.90
1986	91.60	17.27	6.91	115.77	0.65	179.04

* Constant landings (kg) assumed for years 1972–1986, based on landings in 1978 (Manooch et al., 1981).

† Numbers of fish landed estimated separately (mean weight from headboat landings not used). Landings for 1972–1978 were assumed to be very small and set to zero for this analysis. Landings for 1981–1983 were set equal to average of 1979–1980 and 1984–1986.

studies show neither long range migrations nor extensive local movements of adult (> 1 yr) red porgy (Manooch and Hassler, 1978). Nor is there circumstantial or anecdotal information to suggest substantial movements. Thus, even though red porgy are continuously distributed from Cape Hatteras to South Florida and beyond, the range may be subdivided as is convenient and practical and analyses for any chosen area concerning growth, mortality, yield per recruit and other characteristics of adult stocks are valid. We chose to deal with landings and stocks only in and off North Carolina and South Carolina because red porgy are far less abundant in catches off Georgia and Florida, because both the commercial and recreational fisheries of North Carolina and South Carolina are somewhat isolated from similar Florida fisheries, and because our most extensive data set (begun in 1972) is from that area.

With respect to sources of recruitment and consequent analyses such as determination of spawner-recruit relationships, our contention of a Carolina stock is less defensible. Red porgy eggs and larvae are pelagic, are believed to survive transport by ocean currents for 30 days or more (Manooch et al., 1981), and could provide recruitment to the population off North Carolina and South Carolina from the Atlantic shelf of Florida, or even the Gulf of Mexico. Given the highly variable current patterns on the southern U.S. Atlantic shelf (Pietrafesa et al., 1985), the source of zygotes and larvae could vary markedly from year to year. On average, we propose that zygotes from a proximal spawning are more likely to contribute to local recruitment than are those from distant spawning and, that on the whole, the Carolina stock produces its own recruits. If any of the conjectured strategies for maintaining zygotes of reef fish within local populations (e.g., spawning at certain tide stages) are employed by red porgy, then a stronger argument can be made for multigenerational stock integrity.

Peak spawning occurs from March through April, with first maturation for females at age 2 (Manooch et al., 1981). Eggs are pelagic, spherical, and hatch 28 to 38 h after fertilization. Red porgy attain their maximum size slowly and live relatively long (15 yr or older). Females predominate at smaller size intervals,

Table 2. Estimates of commercial landings of red porgy from North and South Carolina, mean weight, and landings in numbers

Year	Landings in biomass			Mean weight (kg)	Landings in numbers (10 ³)
	NC	SC	Total		
1972	1.03	12.38	13.40	1.26	10.60
1973	4.58	8.61	13.18	1.26	10.43
1974	13.25	1.97	15.22	1.26	12.04
1975	14.16	5.39	19.55	1.26	15.47
1976	4.85	41.81	46.66	1.14	40.89
1977	7.57	68.87	76.45	1.43	53.39
1978	64.50	100.06	164.56	1.25	131.33
1979	161.59	161.03	322.62	1.21	266.85
1980	170.18	171.39	341.57	1.23	277.93
1981	276.14	199.36	475.50	1.18	403.31
1982	337.09	197.48	534.57	1.07	501.00
1983	330.14	124.03	454.16	0.93	486.25
1984	211.55	105.72	317.27	0.89	357.69
1985	178.66	53.09	231.75	0.94	247.59
1986	169.51	76.36	245.87	0.85	289.27

and the existence of individuals with both testicular and ovarian tissue suggests protogyny.

In our assessment, annual age-length keys are applied to length-frequency distributions to estimate annual landings in numbers at age. Dividing landings in weight by appropriate annual mean weights, exhibited in commercial, headboat, private recreational or charter boat fisheries, estimates total numbers caught. Two different virtual population analysis techniques are applied to these data to estimate annual, age-specific population sizes, recruitment to age 1, spawning stock size, fishing mortality rates, and exploitation rates. The primary technique is the linked-cohort method of Murphy (1965), and a second technique for comparative purposes is CAL (Parrack, 1986) which adjusts the VPA to indices of stock abundance. We describe the relationship of spawning stock size with the number of recruits, and estimate spawning stock biomass per recruit for unexploited and exploited stocks. We estimate yield per recruit (Ricker, 1975) using two time periods [low exploitation (1972–1978) and high exploitation (1982–1986)] by incorporating age- and year-specific estimates of the instantaneous fishing mortality rate, F .

METHODS

DATA REDUCTION. Data required for the analyses include: 1) historical landings by fishing type, 2) annual length-frequency distributions by fishing type, and 3) annual age-length keys.

Historical Landings.—Total landings resulted from four sectors of the fishery: commercial, headboat, charter boat, and private recreational (Tables 1 and 2). Commercial landings for “porgy” are available for 1972–1983 by weight and are available for “red porgy” for 1984–1986 by number and weight. These landings were reduced by 10% [based on North Carolina data from 1984–1986 (Mercer et al., 1986; Rohde and Mercer, 1987)] to adjust for species other than red porgy listed as porgy.¹ Headboat landings are available by weight and number from 1972 to 1986 (Dixon and Huntsman, in press). Private boat landings are available in both weight and number for 1979–1980 and 1984–1986.² Private

¹ Kenneth Harris, pers. comm., Beaufort Laboratory Southeast Fisheries Science Center, National Marine Fisheries Service, Beaufort, North Carolina 28516-9722.

² John Witzig, pers. comm., Fisheries Statistics Division, National Marine Fisheries Service, 1335 East-West Highway, Silver Spring, Maryland 20910.

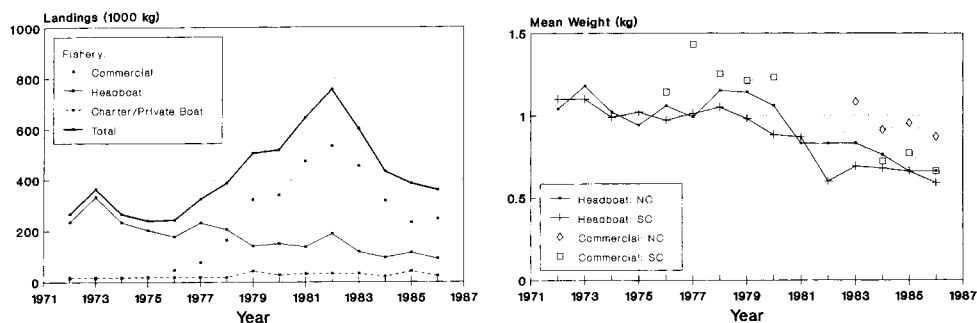


Figure 1 (left). Commercial, headboat combined with charter and private boat, and total landings of red porgy in biomass, 1972–1986.

Figure 2 (right). Mean weight (kg) of red porgy as calculated from length-frequency distributions from headboat and commercial fisheries by state and year.

boat landings are known to be very small and were assumed to be zero for the period 1972–1978, and an average of estimates for 1979–1980 and for 1984–1986 was used for 1981–1983. Charter boat landings were small in the only single year for which they were estimated, 1978 (Manooch et al., 1981), and because the charter fleet has been relatively stable in size and fishing technique we assume a constant weight landed from 1972–1986. Charter boat landings in weight were converted to numbers by dividing that weight by the mean weight of red porgy in the headboat catch (Table 1). Commercial, headboat, and private and charter boat landings are compared in Figure 1.

Commercial landings in weight (Table 2) were converted to landings in numbers by dividing by the annual mean weight per red porgy which were calculated from corresponding length-frequency distributions. Mean weight was calculated directly from the length-frequency distribution by summing the product of the mid-point of each length interval (converted to weight) and the frequency for that length interval and then dividing by the total number of fish. Conversion of length to weight is based on the weight-length relationship in Manooch and Huntsman (1977):

$$W = 0.00002524 (L)^{2.8939} \quad (1)$$

where W equals weight in g, and L equals total length in mm.

Length-Frequency Distributions.—Annual length-frequency distributions are available for each fishing area from the headboat survey for years 1972–1986 (Dixon and Huntsman, in press), and have been combined using a weighted average based on landings in numbers by area for each of these years (Table 3). Annual length-frequency distributions for commercial landings are available from South Carolina landings for 1976–1980³ and 1984–1986,⁴ and for North Carolina landings for 1983–1986 (Mercer et al., 1986; Rohde and Mercer, 1987). Annual sample sizes for available length-frequency distributions for both states combined range between 770 (1979) and 4,989 (1973) from the headboat landings, and between 337 (1983, partial-year from North Carolina) to 6,094 (1985) from commercial landings.

To assist in filling in for missing length-frequencies by state and year, mean weight was calculated from available length frequencies by state and year (both headboat and commercial) using Eq. (1). Mean weight is used as a rough method to compare the length-frequency distributions obtained from headboat and commercial landings and between states (Fig. 2). Mean weight from the headboat fishery track closely between North Carolina and South Carolina. For 1984–1986 when length-frequencies are available from all segments of the commercial and headboat fisheries, mean weights from the North Carolina commercial fishery are uniformly larger than mean weights from South Carolina commercial fishery and from the headboat fishery for both states. Mean weights from the South Carolina commercial fishery from 1976–1980 are also uniformly higher than mean weights from the headboat fishery.

For the commercial fishery length-frequency distributions are available during the 1970s only from South Carolina. Since landings were relatively small in both states during this period, the annual length-frequency distributions from the South Carolina commercial fishery for 1976–1980 were as-

³ South Carolina Marine Resources Research Institute, P.O. Box 12559, Charleston, South Carolina 29412.

⁴ James Zweifel, pers. comm., Science and Research Directorate, Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, Florida 33149.

Table 3. Estimated length-frequency distributions for headboat and commercial landings of red porgy, 1972-1986

Length class (mm)	Fishing year														
	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986
N	4,230	4,989	3,573	2,253	2,340	2,120	1,256	770	1,331	991	2,342	2,181	2,422	1,712	1,690
Headboat															
<225	0.001	0.001	0.001	0.003	0.004	0.0	0.002	0.0	0.001	0.001	0.006	0.005	0.002	0.006	0.010
225-249	0.002	0.004	0.007	0.016	0.007	0.001	0.004	0.002	0.005	0.013	0.016	0.018	0.010	0.017	0.027
250-274	0.006	0.011	0.014	0.033	0.016	0.004	0.016	0.006	0.016	0.024	0.063	0.037	0.043	0.047	0.078
275-299	0.015	0.018	0.033	0.045	0.030	0.011	0.029	0.050	0.047	0.045	0.143	0.090	0.087	0.101	0.125
300-324	0.029	0.031	0.060	0.062	0.058	0.040	0.057	0.052	0.092	0.092	0.150	0.133	0.147	0.159	0.151
325-349	0.049	0.053	0.079	0.083	0.087	0.097	0.061	0.072	0.103	0.127	0.145	0.146	0.153	0.177	0.159
350-374	0.080	0.070	0.106	0.103	0.094	0.130	0.050	0.079	0.118	0.158	0.110	0.147	0.153	0.148	0.144
375-399	0.114	0.096	0.117	0.097	0.121	0.128	0.119	0.094	0.115	0.134	0.107	0.109	0.132	0.129	0.112
400-424	0.163	0.150	0.140	0.133	0.142	0.155	0.124	0.122	0.104	0.117	0.089	0.098	0.101	0.087	0.080
425-449	0.188	0.151	0.134	0.124	0.146	0.143	0.164	0.138	0.122	0.099	0.066	0.082	0.065	0.057	0.051
450-474	0.178	0.158	0.123	0.119	0.120	0.130	0.150	0.147	0.113	0.072	0.045	0.054	0.047	0.038	0.037
475-499	0.096	0.109	0.081	0.076	0.074	0.088	0.102	0.161	0.084	0.067	0.028	0.033	0.026	0.015	0.013
500-524	0.048	0.072	0.058	0.053	0.050	0.046	0.067	0.051	0.041	0.025	0.017	0.029	0.015	0.008	0.007
525-549	0.017	0.043	0.025	0.029	0.032	0.017	0.022	0.020	0.017	0.016	0.008	0.013	0.007	0.007	0.003
550-574	0.008	0.022	0.010	0.016	0.012	0.007	0.018	0.004	0.013	0.006	0.003	0.003	0.002	0.001	0.001
575-599	0.004	0.009	0.005	0.002	0.006	0.002	0.008	0.002	0.004	0.001	0.002	0.001	0.003	0.002	0.0
>599	0.002	0.002	0.004	0.006	0.003	0.001	0.007	0.0	0.005	0.003	0.002	0.002	0.007	0.001	0.002
Commercial															
N	-	-	-	-	1,351	1,694	2,016	2,365	1,429	-	-	(337)	5,145	6,094	5,725
<225	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001	0.002	0.002	0.003	0.0	0.001
225-249	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.001	0.001	0.002	0.002	0.0	0.002
250-274	0.001	0.001	0.001	0.001	0.0	0.0	0.0	0.003	0.001	0.005	0.009	0.013	0.017	0.005	0.011
275-299	0.002	0.002	0.002	0.002	0.001	0.0	0.003	0.005	0.001	0.011	0.021	0.030	0.040	0.017	0.042
300-324	0.017	0.017	0.017	0.017	0.018	0.003	0.017	0.023	0.024	0.036	0.056	0.075	0.095	0.068	0.112
325-349	0.030	0.030	0.030	0.030	0.032	0.009	0.021	0.042	0.045	0.049	0.068	0.087	0.107	0.114	0.122
350-374	0.066	0.066	0.066	0.066	0.084	0.034	0.054	0.064	0.093	0.088	0.110	0.133	0.155	0.165	0.166
375-399	0.086	0.086	0.086	0.086	0.108	0.069	0.078	0.075	0.099	0.099	0.112	0.126	0.139	0.150	0.132
400-424	0.170	0.170	0.170	0.170	0.189	0.150	0.175	0.154	0.182	0.167	0.165	0.162	0.160	0.141	0.152
425-449	0.126	0.126	0.126	0.126	0.142	0.112	0.140	0.124	0.115	0.117	0.107	0.097	0.087	0.119	0.097
450-474	0.190	0.190	0.190	0.190	0.200	0.183	0.212	0.208	0.149	0.163	0.135	0.108	0.080	0.096	0.070
475-499	0.103	0.103	0.103	0.103	0.108	0.127	0.099	0.107	0.072	0.088	0.073	0.058	0.043	0.048	0.037
500-524	0.098	0.098	0.098	0.098	0.067	0.126	0.110	0.110	0.080	0.081	0.065	0.048	0.031	0.036	0.024
525-549	0.039	0.039	0.039	0.039	0.020	0.067	0.040	0.034	0.035	0.035	0.030	0.026	0.021	0.024	0.013
550-574	0.042	0.042	0.042	0.042	0.010	0.080	0.032	0.036	0.049	0.034	0.026	0.018	0.010	0.007	0.010
575-599	0.015	0.015	0.015	0.015	0.010	0.025	0.012	0.009	0.020	0.012	0.009	0.006	0.003	0.006	0.005
>599	0.015	0.015	0.015	0.015	0.011	0.015	0.007	0.006	0.035	0.013	0.011	0.009	0.007	0.004	0.004

Table 4. Age-length keys for red porgy for two time periods (1972–1974 and 1986)

Length class (mm)	Age (years)									
	1	2	3	4	5	6	7	8	9	10+
1972–1974 (N = 1,913)										
<225	1.0	0	0	0	0	0	0	0	0	0
225–249	0.667	0.333	0	0	0	0	0	0	0	0
250–274	0.250	0.750	0	0	0	0	0	0	0	0
275–299	0	0.833	0.167	0	0	0	0	0	0	0
300–324	0	0.469	0.500	0.031	0	0	0	0	0	0
325–349	0	0.131	0.595	0.226	0.048	0	0	0	0	0
350–374	0	0.007	0.350	0.531	0.112	0	0	0	0	0
375–399	0	0	0.079	0.516	0.400	0.005	0	0	0	0
400–424	0	0	0.008	0.276	0.644	0.067	0.004	0	0	0
425–449	0	0	0	0.027	0.596	0.358	0.019	0	0	0
450–474	0	0	0	0.010	0.259	0.502	0.219	0.010	0	0
475–499	0	0	0	0	0.064	0.189	0.494	0.253	0	0
500–524	0	0	0	0	0.010	0.021	0.268	0.309	0.258	0.134
525–549	0	0	0	0	0	0.051	0.120	0.145	0.290	0.393
550–574	0	0	0	0	0	0	0.075	0.113	0.075	0.737
575–599	0	0	0	0	0	0	0	0	0.059	0.941
>599	0	0	0	0	0	0	0	0	0.167	0.833
1986 (N = 524)										
<225	1.0	0	0	0	0	0	0	0	0	0
225–249	0.737	0.263	0	0	0	0	0	0	0	0
250–274	0.231	0.744	0.025	0	0	0	0	0	0	0
275–299	0.045	0.758	0.197	0	0	0	0	0	0	0
300–324	0	0.302	0.628	0.070	0	0	0	0	0	0
325–349	0	0.071	0.471	0.386	0.071	0	0	0	0	0
350–374	0	0	0.267	0.573	0.160	0	0	0	0	0
375–399	0	0	0.065	0.544	0.391	0	0	0	0	0
400–424	0	0	0	0.261	0.652	0.087	0	0	0	0
425–449	0	0	0	0.061	0.455	0.424	0.061	0	0	0
450–474	0	0	0	0	0.100	0.650	0.250	0	0	0
475–499	0	0	0	0	0	0.111	0.556	0.333	0	0
500–524	0	0	0	0	0	0	0.125	0.625	0.250	0
525–549	0	0	0	0	0	0	0	0	1.0	0
550–574	0	0	0	0	0	0	0	0	0	1.0
575–599	0	0	0	0	0	0	0	0	0	1.0
>599	0	0	0	0	0	0	0	0	0	1.0

summed representative of commercial fisheries in both states for those years. For 1984–1986, when length-frequency distributions from commercial fisheries in both states were available, a weighted mean of the length-frequency distributions was calculated with the weighting based on landings in numbers.

Missing length-frequency distributions from commercial landings for fishing years 1972–1975 and 1981–1983 were treated in two different ways, with only the results from the first treatment presented (Table 3). Treatment 1: The unweighted mean of the length-frequency distributions for 1976 through 1980 (each normalized or summed to one) was used for 1972–1975, while incremental changes between normalized length-frequency distributions for 1980 and 1984 (0.25, 0.5, 0.75) were used for 1981–1983 (e.g., for 1981 we used the sum of 75% of the normalized 1980 length-frequency distribution and 25% of the normalized 1984 length-frequency distribution). Treatment 2: The length-frequency distribution from 1976 was used for 1972–1975, and incremental changes between the normalized length-frequency distributions of 1980 and 1983 (0.33, 0.67) were used for 1981 and 1982 while the partial-year distribution for 1983 from North Carolina was used for 1983. The analytical results should be insensitive to the two different treatments for 1972–1975, because commercial landings for these years were small in comparison to headboat landings. However, analytical results would be expected

Table 5. Estimated numbers of red porgy landed by age and the total weight landed in North and South Carolina, 1972-1986

Age	Numbers by year (10 ³)														
	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986
1	0.9	2.0	2.3	5.4	2.8	0.4	1.7	0.8	1.7	4.0	13.9	9.1	7.3	8.5	11.6
2	9.0	14.6	20.2	26.0	16.9	9.8	14.4	16.8	21.3	32.9	95.5	61.5	57.1	54.9	62.8
3	20.2	26.5	33.7	32.8	30.2	32.1	24.2	33.7	48.7	76.1	126.5	107.0	101.5	99.2	98.1
4	39.8	47.0	47.4	43.0	46.2	55.6	45.9	60.5	82.4	131.7	160.4	147.2	136.3	127.5	120.2
5	78.7	91.1	71.6	64.2	71.1	80.0	86.8	104.1	111.6	159.7	174.7	147.3	121.8	103.8	96.7
6	45.5	54.0	36.8	34.7	38.8	45.1	59.6	79.0	67.3	86.4	94.3	73.5	50.9	45.7	39.7
7	26.0	38.0	24.1	22.7	23.3	29.6	38.6	57.2	42.0	57.1	55.0	40.4	25.3	20.8	17.3
8	11.0	19.4	12.0	11.8	11.8	16.0	22.3	33.9	26.0	37.9	35.2	26.3	15.1	11.7	9.5
9	4.7	10.9	6.5	6.9	7.1	8.6	12.7	17.3	17.3	22.6	23.7	19.2	11.8	9.9	6.3
10+	6.6	17.3	9.3	10.0	9.0	11.4	16.2	18.4	34.1	28.5	27.5	17.8	10.1	5.5	6.0
Total numbers (10 ³):	242.4	320.7	264.0	257.4	257.3	288.6	322.5	421.7	452.5	595.1	806.7	649.4	537.2	487.5	468.4
Total biomass (10 ³ kg):	266.0	364.6	265.8	239.4	242.6	325.4	387.5	505.1	518.8	644.0	755.4	602.1	434.0	386.5	361.7

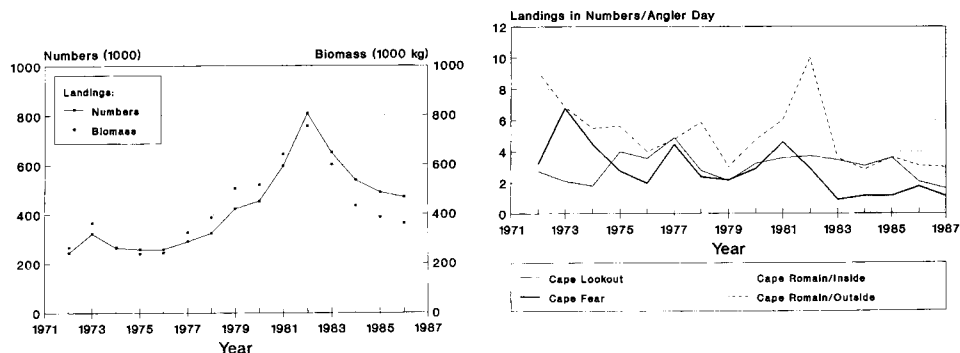


Figure 3 (left). Total landings of red porgy in numbers and biomass, 1972–1986.

Figure 4 (right). Catch-per-unit-effort from headboat data base in numbers of fish caught per angler day from four fishing areas: Cape Lookout (CLT), Cape Fear (CFR), Cape Romain Inside (CRI), and Cape Romain Outside (CRO).

to be more sensitive to the assumptions imbedded in the two treatments for 1981–1983. Both treatments assume a linear progression in the underlying length-frequency distributions either for the period 1980–1984 (treatment 1) or for the period 1980–1983 with limited 1983 North Carolina data assumed representative for both North and South Carolina (treatment 2).

No length-frequency distributions exist for the charter boat or private recreational fisheries. We assumed length-frequency distributions from the headboat fishery were representative of the smaller recreational fisheries.

Age-Length Keys.—Two age-length keys are available (Table 4), one based on 1,913 red porgy collected during 1972–1974 (Manooch and Huntsman, 1977), and another based on 524 red porgy collected during 1986 [and aged using scales in the same manner described in Manooch and Huntsman (1977)]. In both, data for the few fish that are age 10 and older are pooled into a single age group. Separate age-length keys for each year from 1975 through 1985 were estimated from the keys for 1972–1974 and 1986 by incremental progression between these two keys based on the difference between corresponding matrix elements (proportions) divided by 12. Age-frequencies were computed from length frequencies by grouping fish of known age by 25-mm length intervals, calculating the percentage of fish of each observed age in each group, and using these percentages to estimate the number of fish of each age for the unaged group (Ricker, 1975).

Catch-at-Age Matrix.—Landings in numbers are converted to landings in numbers at age by the matrix equation:

$$N_{ax1} = n \cdot A_{axb} \cdot L_{bx1}, \quad (2)$$

where N is the vector of landings in numbers for ages 1 through a (e.g., $a = 10$), n is the number of red porgy landed (a scalar), A is the age-length key, and L is the length-frequency distribution (vector) with b length classes (e.g., $b = 17$). This equation was applied separately to commercial and headboat landings in numbers annually (Table 5). Charter and private boat landings in numbers were combined with headboat landings prior to the annual application of Eq. (2). Annual variation in red porgy landings in numbers and weight are compared in Figure 3.

DATA ANALYSES. We estimate age-specific population sizes and mortality rates through virtual population analysis applied to landings in numbers at age, describe the spawner-recruit relationship and spawning stock ratio, and calculate yield-per-recruit.

Virtual Population Analysis (VPA).—Age-specific estimates of population size and instantaneous fishing mortality rates (F) were obtained from annual, age-specific landings data (1972–1986) using two methods: 1) linked-cohort (Murphy, 1965), and 2) CPUE-tuned (Parrack, 1986). Both VPAs were applied to ages 1–9. Slopes of the catch curve for the 1977 and 1978 year classes (age-6 through age-9) were estimated by the method of Chapman and Robson (1960; see Seber, 1973) and averaged to denote the final Z (1.032) for these 2-year classes. Final F was calculated from the final Z by subtracting M , the instantaneous natural mortality rate (assumed constant for all ages in the analyses) which ranges from 0.2 to 0.35 (Huntsman et al., 1983). For a median value we chose an M of 0.28 (using method of Hoenig 1983) and conducted a linked-cohort VPA each for high, low, and median natural mortality.

Table 6. Estimates of population numbers of red porgy by age (1–10) and total for years 1972–1986 [M = 0.28, based on Murphy's (1965) linked-cohort method]

Year	Population numbers by age (10 ⁶)										Total
	1	2	3	4	5	6	7	8	9	10	
1972	2.15	1.36	0.93	0.63	0.44	0.26	0.14	0.08	0.03	0.02*	6.04
1973	2.23	1.62	1.02	0.68	0.45	0.26	0.16	0.09	0.05	0.02	6.58
1974	2.22	1.68	1.21	0.75	0.47	0.26	0.15	0.09	0.05	0.03	6.92
1975	2.09	1.68	1.26	0.89	0.52	0.30	0.16	0.10	0.06	0.03	7.08
1976	1.95	1.58	1.25	0.92	0.63	0.34	0.19	0.10	0.06	0.04	7.07
1977	1.86	1.47	1.18	0.92	0.66	0.42	0.22	0.13	0.07	0.04	6.96
1978	1.74	1.41	1.10	0.86	0.64	0.43	0.28	0.14	0.08	0.04	6.73
1979	1.61	1.32	1.05	0.81	0.61	0.41	0.27	0.18	0.09	0.05	6.40
1980	1.50	1.21	0.98	0.76	0.56	0.37	0.24	0.16	0.10	0.05	5.95
1981	1.35	1.13	0.90	0.70	0.51	0.33	0.22	0.15	0.10	0.06	5.45
1982	1.12	1.02	0.83	0.62	0.43	0.26	0.17	0.12	0.08	0.05	4.70
1983	0.91	0.83	0.69	0.52	0.33	0.18	0.11	0.08	0.06	0.04	3.76
1984	0.73	0.68	0.58	0.43	0.26	0.12	0.07	0.05	0.04	0.03	3.00
1985	0.60	0.55	0.47	0.35	0.21	0.09	0.05	0.03	0.03	0.02	2.39
1986	0.58	0.45	0.37	0.27	0.15	0.07	0.03	0.02	0.01	0.01	1.96

* Estimated from regression of age-10 population size on age-9 population size for years 1973–1978 ($r = 0.92$).

For the linked-cohort method, each F for age-8 was assumed equal to F for age-9 during the same fishing year for all year classes 1963 through 1978 (Prager and MacCall, 1988). The program MURPHY (Abramson, 1971), based on Tomlinson (1970), is applied separately to each cohort. For example, the VPA for the 1977 year class (starting with age 9 in 1986) provides an estimate of F for age 8 in 1985 (same year class) which is assumed equal to F for age 9 in 1985 (1976 year class).

Another VPA method (separable VPA) is used to estimate the final F for year classes more recent than the 1978 year class (partial cohorts). This method assumes that the instantaneous fishing mortality rate can be decomposed into the product of an age component common to all years and a year component common to all ages (Doubleday, 1976). The age component for the final fishing year (1986), estimated using Pope and Shepherd's (1982) algorithm modified for the microcomputer,³ was applied to catch data for 1982–1986 during which the fishing pattern appears to be relatively consistent. This age component multiplied by F for age 9 in 1986 was used to estimate final F for each of the partial cohorts ending in 1986.

The second major VPA approach applied to the full catch matrix (1972–1986) utilizes additional information on indices of stock abundance to guide the process of back calculating age-specific population size and fishing mortality from the catch matrix (Deriso et al., 1985; Pope and Shepherd, 1985). Parrack (1986) developed a computer program (CAL) that uses an estimate of natural mortality (e.g., $M = 0.28$) and age-specific fishing mortality rates for the final fishing year (using estimates obtained from separable VPA above). Multiple indices of stock abundance can be used in CAL effectively (Collie, 1988; Vaughan et al., 1988). With red porgy the only available indices of stock abundance are based on area-specific estimates of catch-per-unit effort (CPUE) from the headboat fishery. Fishing effort in angler days is available from four headboat fishing areas (Cape Lookout, Cape Fear, Cape Romain Inshore, and Cape Romain Offshore) (Dixon and Huntsman, in press). CPUE (based on all ages 1 and older in the landings) for these four areas are compared in Figure 4. For the initial runs of CAL three of the four indices correlate well with the "best" population estimates (>80% probability of significance for Cape Fear, Cape Romain Inshore, and Cape Romain Offshore). CAL was then rerun with only these three CPUE indices. The purpose of these computer runs with CAL was to explore the sensitivity of applying VPA under the different assumptions of the linked-cohort and CAL methods.

Age-specific population estimates in numbers of red porgy are summarized for fishing years 1972–1986 (Table 6). Biomass at age was calculated from the von Bertalanffy equation [Manooch and Huntsman, 1977; L is total length (mm) and t is age (yr)]

$$L = 763.0(1 - \exp(-0.096(t + 1.88))) \quad (3)$$

³ Douglas Clay, pers. comm., Marine and Anadromous Fisheries Division, Gulf Fisheries Center, Fisheries and Ocean Canada, Moncton, N.B. E1C 9B6, Canada.

Table 7. Estimates of population biomass of red porgy by age (1–10) and total for years 1972–1986 [$M = 0.28$, based on Murphy's (1965) linked-cohort method]

Year	Population biomass by age (kg · 10 ⁶)										Total
	1	2	3	4	5	6	7	8	9	10	
1972	0.18	0.24	0.28	0.29	0.28	0.22	0.15	0.10	0.05	0.03	1.82
1973	0.19	0.29	0.31	0.31	0.28	0.22	0.17	0.11	0.07	0.04	1.98
1974	0.19	0.30	0.37	0.34	0.30	0.21	0.16	0.11	0.07	0.05	2.10
1975	0.18	0.30	0.38	0.40	0.33	0.25	0.17	0.12	0.08	0.05	2.26
1976	0.17	0.28	0.38	0.42	0.40	0.28	0.20	0.13	0.09	0.06	2.41
1977	0.16	0.26	0.36	0.42	0.42	0.35	0.23	0.16	0.10	0.07	2.52
1978	0.15	0.25	0.33	0.39	0.41	0.35	0.29	0.18	0.12	0.08	2.55
1979	0.14	0.23	0.32	0.37	0.39	0.34	0.28	0.22	0.13	0.09	2.51
1980	0.13	0.21	0.30	0.35	0.36	0.31	0.25	0.20	0.15	0.09	2.34
1981	0.12	0.20	0.27	0.32	0.32	0.27	0.23	0.19	0.14	0.11	2.17
1982	0.10	0.18	0.25	0.28	0.27	0.21	0.18	0.15	0.12	0.09	1.84
1983	0.08	0.15	0.21	0.23	0.21	0.15	0.12	0.11	0.09	0.07	1.41
1984	0.06	0.12	0.17	0.19	0.17	0.10	0.07	0.07	0.06	0.05	1.07
1985	0.05	0.10	0.14	0.16	0.13	0.08	0.05	0.04	0.04	0.04	0.82
1986	0.05	0.08	0.11	0.12	0.10	0.06	0.03	0.03	0.02	0.02	0.61

for age in years plus 0.5 (to account for mid-season effects) and converted to weight using Eq. (1) (Table 7, Fig. 5). Population biomass was obtained by summing over ages 1–10.

Age-specific estimates of fishing mortality rates from the linked-cohort method ($M = 0.28$) for fishing years 1972–1986 are presented (Table 8). Temporal trends in mean annual F for the three levels of natural mortality are illustrated in Figure 6. Age-specific exploitation rates were calculated by dividing the landings in numbers at age by the number of that age in the population at the start of the fishing year. Average exploitation rates were calculated for two time periods (1972–1978 and 1982–1986) to represent two different fishing regimes (Table 9).

Deviations in population estimates between our two treatments (different assumptions on length-frequency distributions from commercial landings for 1972–1975 and 1981–1983) were found to be very similar for 1972 through 1983 (Table 10). However, relatively large deviations are noted in recruitment at age-1 for 1983–1986 and in population size estimates (numbers and biomass) in 1985 and 1986.

Furthermore, greater error is likely for the parameters (e.g., age-specific population size and F) estimated for recent fishing years (e.g., 1985–1986) and for older age classes (e.g., age 7–9). The rate of convergence to the true estimates depends on the cumulative mortality rate ($Z = M + F$) as one works back in time, with quicker convergence for higher Z (Pope, 1972; Ulltang, 1977). The sensitivity of estimated age-specific population size to final F was investigated using separable VPA. As expected it takes about 5–6 years for estimates from a VPA to converge (Fig. 7), so that estimates of population size or F for the most recent years used in the analysis should be viewed with some skepticism.

Spawner-Recruit Relationships.—Establishing the relationship between spawning stock and recruitment to the fishery can be valuable to understanding the dynamics of the stock and to its management. If no relationship exists, controlling fishing mortality for the purpose of protecting spawning stock biomass will not necessarily lead to improved catches from subsequent generations. The manager can only assure the survival of some minimum number of spawners and preserve the quality of pre-recruit habitat.

To evaluate the spawner-recruit relationship, we made the following assumptions: Spawning begins at age-2 with about 37% mature females, 81% of age-3, and 100% of age-4 and older (Manooch and Huntsman, 1977). Age-specific sex ratios were approximated from size-specific sex ratios given in Manooch, 1976. The decline in the proportion of females for ages 2 through 10 as follows: 0.97 (age 2), 0.94 (age 3), 0.89 (age 4), 0.84 (age 5), 0.53 (age 6), 0.41 (age 7), and 0.40 (age 8–10). We estimated the spawning population for the years 1972–1985 in numbers and biomass for three levels of M using the linked-cohort VPA and for one level of M using CAL (Table 11). Comparisons of spawners and recruits are shown between VPA approaches (Fig. 8a) and among assumed natural mortality (Fig. 8b).

Gabriel et al. (1990) suggest the ratio of lifetime reproductive potential of an average recruit in the form of spawning stock biomass with and without fishing mortality as a biological reference point for the management of fish stocks. This method does not account for changes in growth rates, age at first maturity, fecundity or other means of population regulation that may occur as fishing or other man-

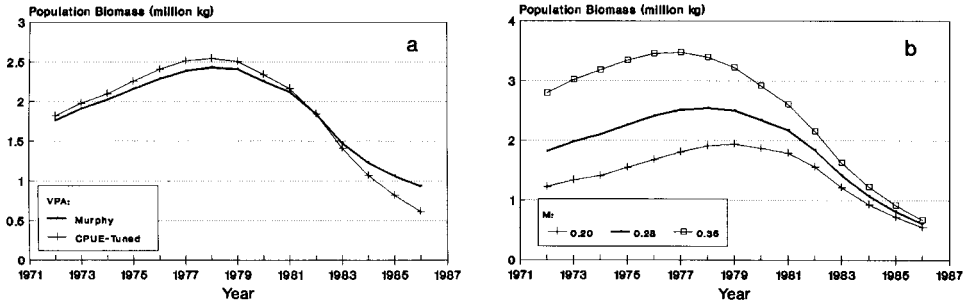


Figure 5. Total population size in biomass (ages 1–10) of red porgy based on (a) two types of virtual population methods (Murphy linked-cohort, and CPUE-Tuning; with $M = 0.28$) and (b) three levels of natural mortality ($M = 0.20, 0.28$, and 0.35 ; with Murphy linked-cohort VPA), 1972–1986.

induced mortality increases. However, this spawning stock ratio (SSR) is currently used by the South Atlantic and Gulf of Mexico Fishery Management Councils as the basis for definition of overfishing, usually with values ranging from 20% to 40%. Results based on spawning stock biomass, as opposed to potential egg production, are calculated from VPA estimates of fishing mortality (Table 8) for fishing years 1972–1986 (Fig. 9a) and for year classes 1971–1980 (Fig. 9b). SSR is based either strictly on female biomass (using sex ratios presented earlier), or on both sexes combined to address the potential problem of a lack of male gametes. This latter problem could arise with high fishing mortality, preventing sufficient numbers of female red porgy to change to male red porgy at older, mature ages.

Yield-per-Recruit Analysis.—Yield-per-recruit models allow the measure of efficiency of different harvest strategies resulting from varying F and the minimum age at recruitment to the fishery. In this analysis a Ricker-type model (Ricker, 1975), permitting the use of age-specific estimates of F available from VPA. As a result, incremental F -multiples (age-vector of F) are used in place of incremental F (constant across all age classes). An F -multiple of 1.0 represents base conditions for either 1972–1978 or 1982–1986. Estimates of yield per recruit are summarized for a range of F -multiples (based on the linked-cohort VPA) and age at entry for two time periods and three levels of M (Table 12, Fig. 10).

RESULTS

Historical Data.—Total landings of red porgy off the Carolinas increased from 266,000 kg in 1972 to a peak of 755,000 kg in 1982, and rapidly declined to

Table 8. Estimates of age-specific and unweighted mean fishing mortality rates for red porgy off the Carolinas for years 1972–1986 based on a linked-cohort (Murphy, 1965) virtual population analysis with $M = 0.28$. Note: Linkage assumption is: $F_8 = F_9$

Year	Age									Mean
	1	2	3	4	5	6	7	8	9	
1972	0.001	0.008	0.025	0.074	0.228	0.219	0.232	0.180	0.180	0.127
1973	0.001	0.011	0.030	0.082	0.266	0.265	0.315	0.298	0.298	0.174
1974	0.001	0.014	0.033	0.075	0.189	0.177	0.197	0.169	0.169	0.114
1975	0.003	0.018	0.030	0.057	0.151	0.143	0.173	0.152	0.152	0.098
1976	0.002	0.012	0.028	0.059	0.137	0.139	0.147	0.140	0.140	0.089
1977	0.000	0.008	0.032	0.072	0.150	0.132	0.163	0.155	0.155	0.096
1978	0.001	0.012	0.025	0.063	0.167	0.174	0.174	0.194	0.194	0.112
1979	0.001	0.015	0.037	0.089	0.216	0.247	0.275	0.249	0.249	0.153
1980	0.001	0.020	0.058	0.131	0.256	0.231	0.220	0.212	0.212	0.149
1981	0.004	0.033	0.092	0.207	0.393	0.361	0.334	0.315	0.315	0.228
1982	0.015	0.113	0.192	0.347	0.616	0.533	0.446	0.401	0.401	0.341
1983	0.011	0.088	0.195	0.393	0.700	0.641	0.509	0.439	0.439	0.379
1984	0.011	0.101	0.224	0.449	0.738	0.623	0.528	0.398	0.398	0.386
1985	0.016	0.122	0.278	0.534	0.835	0.780	0.632	0.553	0.553	0.478
1986	0.023	0.175	0.364	0.711	1.197	1.072	0.889	0.752	0.752	0.659

Table 9. Estimates of age-specific and mean (ages 1–10) fishing exploitation rates on red porgy in North and South Carolina for two time periods, 1972–1978 and 1982–1986, and three levels of instantaneous natural mortality rate, $M = 0.20$, 0.28 , and 0.35 [based on Murphy's (1965) linked-cohort method]

Ages (years)	Time periods		Ratio*
	1972-1978	1982-1986	
M = 0.20			
1	0.002	0.017	8.5
2	0.016	0.119	7.4
3	0.038	0.223	5.9
4	0.083	0.376	4.5
5-10	0.209	0.495	2.4
1-10	0.063	0.229	3.6
M = 0.28			
1	0.001	0.013	13.0
2	0.010	0.098	9.8
3	0.025	0.193	7.7
4	0.058	0.336	5.8
5-10	0.153	0.444	2.9
1-10	0.041	0.193	4.7
M = 0.35			
1	0.001	0.011	11.0
2	0.007	0.083	11.9
3	0.017	0.169	9.9
4	0.040	0.303	7.6
5-10	0.109	0.400	3.7
1-10	0.027	0.164	6.1

* Ratio of fishing exploitation rates for period 1982–1986 to 1972–1978.

about 362,000 kg in 1986 (Fig. 1). Headboat landings generally declined from a maximum of 235,000 kg in 1973 to a minimum of 93,000 kg in 1986. Commercial landings were small until 1978 (less than 15,000 kg), when they rapidly rose to a peak of 337,000 kg in 1982, and then declined to 283,000 kg in 1986.

In general, trends in landings in numbers closely follow the trends in landings in weight (Fig. 3), with the primary exception that landings in weight declined more rapidly for 1984–1986 because fish were smaller. As with landings in weight, landings in numbers (Table 5) were low from 1972–1978, peaked at 807,000 in 1982, and decreased to 468,000 in 1986.

Age 5 contribute most to landings in numbers for 1972–1983, and age 4 pre-dominate for 1984–1986 (Table 5). However, significant contribution is made by all ages 3–7. We assume that ages 5 and older are fully recruited for 1972–1986.

Virtual Population Analysis.—Annual trends in fishing mortality, recruits, and spawning stock size should be viewed with some care. Because of the linear smoothing in the age-length keys between 1972–1974 and 1986, there is the potential for smoothing of the VPA output. To what extent is unknown, so confidence is greater in the magnitude, rather than temporal trend, in output variables.

For the linked-cohort VPA with an intermediate level of natural mortality ($M = 0.28$), population estimates rose from 6.0 million red porgy (age 1 and older) in 1972 to 7.1 million in 1975, and declined steadily to 2.0 million in 1986 (Table 6). Similarly, population biomass (age 1 and older) rose from 1.8 million kg in 1972 to 2.5 million kg in 1978, and declined steadily to 0.6 million kg in 1986 (Table 7). Different M values resulted in slightly different peak years ($M = 0.20$,

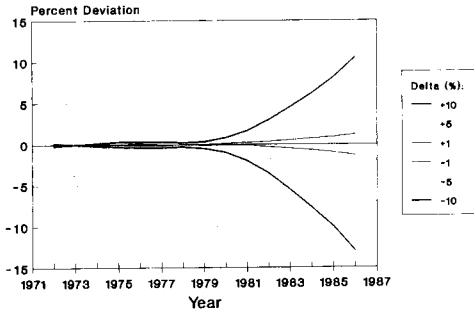
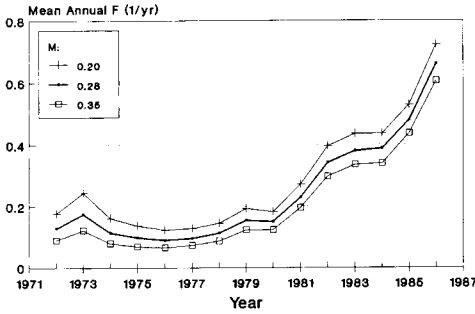


Figure 6 (left). Mean annual fishing mortality rates (ages 1–9) of red porgy at three levels of natural mortality ($M = 0.20, 0.28$, and 0.35 ; based on linked-cohort VPA), 1972–1986.

Figure 7 (right). Percent deviation in estimated population numbers for age 1 red porgy with fixed deviations in final F [for age 9 in 1986, $M = 0.28$, based on separable virtual population analysis (Pope and Shepherd, 1982)].

1.9 million kg in 1979; $M = 0.35$, 3.5 million kg in 1977), but the minima were in the same year, 1986 ($M = 0.20$, 0.5 million kg; $M = 0.35$, 0.7 million kg) (Fig. 5b). Greater assumed natural mortality resulted in higher population estimates.

Only small differences are noted between estimates from the linked-cohort method of Murphy (1965) and the CPUE-tuning program CAL, indicating that there is little disagreement between the results from the catch-at-age matrix and trends in the headboat CPUE indices. This is probably due to the relative constancy of these indices (Cape Fear and both Cape Romain indices) during 1983–1986 when tuning has its greatest effect on VPA estimates (Fig. 4).

For both VPA methods, age-specific exploitation rates were lowest for age 1, increased through age 4, and were highest for ages 5 and older (Table 9 shows results from linked-cohort VPA). Mean annual exploitation rates were generally low for the period 1972–1980, and rose through the 1980s (Fig. 6). Depending

Table 10. Percent deviation in population variables (population size of age 1, total numbers, and total biomass) between treatment 1 and treatment 2 representing two assumptions of commercial length-frequency distributions based on separable VPA

Year	Deviation in final F (%) ^a		
	Age-1 numbers	Total population size	
		Numbers	Biomass
1972	–2.45	–2.05	–2.41
1973	–2.75	–2.29	–2.26
1974	–3.98	–2.92	–2.60
1975	–2.26	–2.83	–2.80
1976	3.20	–1.27	–2.59
1977	1.98	–0.43	–2.24
1978	–0.16	–0.36	–1.95
1979	–2.93	–1.00	–1.81
1980	–4.43	–1.90	–1.86
1981	–2.03	–2.03	–1.92
1982	–2.92	–0.77	–1.15
1983	11.03	2.85	0.40
1984	22.41	9.57	3.46
1985	33.24	17.60	9.47
1986	34.91	26.57	18.55

^a $P = 100(T_2 - T_1)/T_1$, where P = percent deviation, T_1 is variable for treatment 1, and T_2 is corresponding variable for treatment 2.

Table 11. Estimates of red porgy spawners (ages 2–10) in numbers and biomass, and number of recruits to age-1 for three levels of natural mortality (M) [based on Murphy's (1965) linked-cohort method] and one level of natural mortality (0.28) with CAL (Parrack, 1986) for 1972–1985

Year	Spwaners*		Recruits to age-1† (10 ⁶)
	Numbers (10 ⁶)	Biomass (kg · 10 ⁶)	
VPA = MURPHY, M = 0.20			
1972	1.58	0.72	1.27
1973	1.72	0.77	1.30
1974	1.87	0.82	1.29
1975	2.08	0.92	1.20
1976	2.22	1.02	1.20
1977	2.28	1.09	1.18
1978	2.29	1.12	1.12
1979	2.28	1.13	1.08
1980	2.20	1.09	1.00
1981	2.09	1.04	0.84
1982	1.88	0.92	0.69
1983	1.52	0.72	0.57
1984	1.25	0.57	0.47
1985	1.01	0.45	0.46
VPA = MURPHY, M = 0.28			
1972	2.38	1.04	2.23
1973	2.61	1.12	2.22
1974	2.86	1.21	2.09
1975	3.09	1.34	1.95
1976	3.21	1.45	1.86
1977	3.20	1.50	1.74
1978	3.10	1.49	1.61
1979	2.97	1.45	1.50
1980	2.76	1.36	1.35
1981	2.53	1.25	1.12
1982	2.22	1.07	0.91
1983	1.78	0.83	0.73
1984	1.43	0.65	0.60
1985	1.14	0.50	0.58
VPA = MURPHY, M = 0.35			
1972	3.69	1.55	3.84
1973	4.04	1.69	3.71
1974	4.37	1.82	3.40
1975	4.60	1.96	3.06
1976	4.63	2.05	2.78
1977	4.46	2.06	2.50
1978	4.17	1.98	2.23
1979	3.83	1.86	2.02
1980	3.43	1.68	1.78
1981	3.04	1.49	1.46
1982	2.60	1.24	1.17
1983	2.05	0.95	0.92
1984	1.63	0.73	0.75
1985	1.28	0.56	0.73
VPA = CAL, M = 0.28			
1972	2.34	1.02	2.10
1973	2.53	1.10	2.09
1974	2.73	1.17	2.00
1975	2.92	1.27	1.89
1976	3.03	1.37	1.87
1977	3.03	1.41	1.81
1978	2.97	1.41	1.68

Table 11. Continued

Year	Spawners*		Recruits to age-1† (10 ⁶)
	Numbers (10 ⁶)	Biomass (kg·10 ⁶)	
1979	2.90	1.39	1.58
1980	2.76	1.32	1.47
1981	2.58	1.23	1.31
1982	2.32	1.08	1.22
1983	1.93	0.87	1.11
1984	1.68	0.73	0.99
1985	1.50	0.63	1.00

* Spawners calculated from VPA population estimates with sex ratios and female maturity schedules given in text.

† Year of recruitment to age-1 is year + 1.

on the level of M , exploitation rates for the fully recruited age classes (age 5 and older) ranged from 0.11 to 0.21 for the period 1972–1978 and from 0.40 to 0.49 for the period 1981–1986. Similarly, population exploitation rates (age 1 and older) ranged from 0.03 to 0.06 for the period 1972–1978 and from 0.16 to 0.23 for the period 1982–1986.

Spawner-Recruit Relationships.—For the linked-cohort VPA with $M = 0.28$, spawning stock rose from 2.4 million mature females in 1972 to a peak of 3.2 million mature females in 1976, and declined to 1.1 million mature females in 1986 (Table 11). In biomass, spawning stock rose from 1.0 million kg in 1972 to a peak of 1.5 million kg in 1977, and declined to 0.5 million kg in 1986. Estimates of recruitment to age-1 were obtained directly from the VPA (Table 6 for linked-cohort VPA with $M = 0.28$). Recruitment was highest in the early 1970s peaking in 1973 with 2.2 million recruits (from the 1972 spawning stock), declined to 0.6 million recruits in 1986 (from the 1985 spawning stock). Spawning stock biomass and recruitment estimates from CAL ($M = 0.28$) show a similar pattern (Fig. 8a). Spawning stock biomass estimates peaked at 1.4 million kg in 1977–1978 and declined to 0.6 million kg in 1986, while recruitment to age-1 declined steadily from 2.1 million in 1972 to 1.0 million in 1986.

Abundance of fish of spawning age (2–10) generally paralleled population size (Table 11). Spawning stock peaked in 1977 (3.2 million weighing 1.5 million kg for $M = 0.28$), and declined to a minimum in 1986 (1.1 million red porgy weighing 0.5 million kg for $M = 0.28$). Meanwhile, recruits to age-1 peaked at 2.2 million in 1973 (from the 1972 spawning stock), and declined to a minimum of 0.6 million in 1986 (from the 1985 spawning stock).

Yield-per-Recruit Analysis.—Yield-per-recruit curves are shown for two exploitation regimes (1972–1978 and 1982–1986) using fishing mortality estimates from the linked-cohort VPA with $M = 0.28$ (Fig. 10) and based on growth estimates from Manooch and Huntsman (1977). Realized yield per recruit showed an increase between the low and high exploitation periods (Table 12). Between the two time periods 1972–1978 and 1982–1986, yield per recruit increased from 121.1 g to 184.8 g, an increase of 53%, but the F -multiple of 1.0 for the second period (1982–1986) was equivalent to a total population F (ages 1 and older) of 3.7/yr, or 3.7 times the total F (1.0/yr) for the first period (1972–1978). The increase in F for ages 1–4 (7 times) was substantially greater than for ages 5–9 (3 times). Hence, following the curve at an age at entry of 1.0 to an F -multiple of 3.7 (Fig. 10a) closely matches the more recent base conditions (Fig. 10b).

During the low exploitation period (1972–1978), yield per recruit ranged from

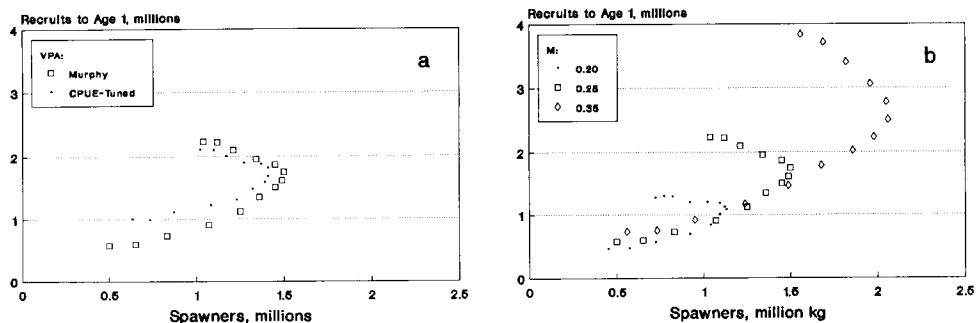


Figure 8. Spawning stock size in biomass (ages 2–10) of red porgy versus recruits to age 1 based (a) on two types of virtual population methods (linked-cohort, and CPUE-Tuning; with $M = 0.28$) and (b) three levels of natural mortality ($M = 0.20, 0.28$, and 0.35 ; with on linked-cohort VPA), 1972–1985.

66.5 g ($M = 0.35$) to 221.1 g ($M = 0.20$), while, for the high exploitation period (1982–1986), it ranged from 137.9 g ($M = 0.35$) to 254.0 g ($M = 0.20$). For the low exploitation period, large increases in yield per recruit (10% to 40%) can be obtained largely by increasing fishing mortality and not by increasing the age at entry (minimum size limits). For the high exploitation period, small increases in yield per recruit (less than 10%) can be obtained by jointly increasing fishing mortality and the age at entry.

Huntsman et al. (1983, Table 2) presented estimates of maximal yield per recruit ranging from 150 g ($M = 0.35$, $F = 0.80$) to 300 g ($M = 0.20$, $F = 0.50$) for constant F 's comparable or larger than for the period 1982–1986. Similar estimates of maximal yield per recruit, based on linked-cohort estimates of F , range from 149 g ($M = 0.35$, mean $F = 0.37$, F -multiple = 2.0, 1982–1986) to 254 g ($M = 0.20$, mean $F = 0.46$, F -multiple = 1.0, 1982–1986).

MANAGEMENT IMPLICATIONS

Moderate catches, primarily by headboat, of red porgy were made off the Carolinas from 1972 through about 1978 (Fig. 1). After about 1978, commercial landings increased rapidly and exceeded headboat landings from 1979 to the present. Very large catches were made from 1979 through 1983, and peaked at 755,000 kg in 1982. A decline, perhaps related to overharvesting, has occurred

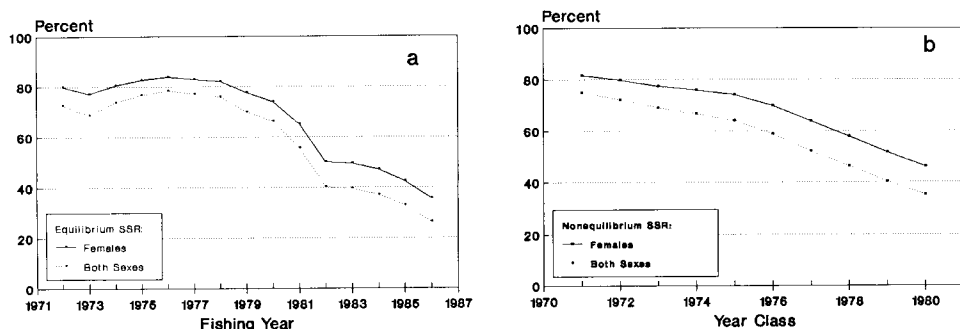


Figure 9. Equilibrium (a) and nonequilibrium (b) estimates of spawning stock ratio of red porgy based on estimates of fishing mortality from the linked-cohort VPA method of Murphy (1965).

Table 12. Estimates of yield per recruit for red porgy for two time periods (1972–1978 and 1981–1986) and three levels of instantaneous natural mortality rate ($M = 0.20, 0.28$, and 0.35) by age-at-entry and F-multiple. For each combination of time period and M , yield per recruit is given in grams for actual conditions (age-at-entry = 1 and F-multiple = 1.0), remaining values are percent change from yield-per-recruit estimates

Natural mortality	Age-at-entry	F-multiple				
		0.2	0.6	1.0	1.4	1.8
1972–1978						
0.20	1	–66.9	–23.7	221.1 g	12.8	19.3
	2	–66.9	–23.7	0.1	12.9	19.6
	3	–67.0	–23.7	0.5	13.7	20.8
	4	–67.6	–24.4	0.4	14.5	22.3
0.28	1	–71.6	–28.9	121.1 g	19.7	33.1
	2	–71.6	–28.9	0.0	19.7	33.2
	3	–71.8	–29.3	0.3	19.6	33.4
	4	–72.5	–30.8	–1.8	18.3	32.3
0.35	1	–74.5	–32.5	66.5 g	25.3	45.1
	2	–74.6	–32.6	–0.1	25.3	45.0
	3	–74.9	–33.2	–0.9	24.3	44.2
	4	–75.9	–35.2	–3.6	21.3	40.9
1982–1986						
0.20	1	–36.9	–2.0	254.0 g	–3.3	–6.9
	2	–36.8	–1.5	1.0	–2.0	–5.3
	3	–36.9	0.9	5.4	3.9	1.6
	4	–38.2	3.0	10.4	10.6	9.5
0.28	1	–47.5	–8.9	184.8 g	1.3	0.5
	2	–47.5	–8.6	0.5	2.0	1.5
	3	–48.1	–8.0	2.6	5.2	5.6
	4	–50.3	–9.1	3.4	7.3	8.7
0.35	1	–54.7	–14.0	137.9 g	5.2	7.2
	2	–54.7	–14.0	0.3	5.7	7.9
	3	–55.7	–14.7	0.4	6.6	9.4
	4	–58.5	–18.1	–2.2	4.9	8.4

since. Age structure has also been affected by the recent high landings, with the age contributing the greatest numbers to the landings decreasing from 5 (1972–1983) to 4 (1984–1986).

Population size peaked in the mid-1970s, and declined to a minimum about 1986 (Fig. 5a). For the period 1972–1978 exploitation rates were low (4.1% for the population and 15.3% for fully recruited age classes for $M = 0.28$), but were much higher for the recent period 1982–1986 (19.3% for the population and 44.4% for fully recruited age classes for $M = 0.28$).

Similar patterns are noted for spawning stock biomass and recruitment to age-1 for M equals 0.20 and 0.35, except that during the 1970s considerably higher recruitment and spawning stock biomass is noted for $M = 0.35$ and considerably lower recruitment and spawning stock size for $M = 0.20$. Loss of spawning stock biomass was appreciable between the low exploitation period and high exploitation period (30–40%) compared to the loss between the unexploited stock and the low exploitation period (15–30%). Further, spawning stock ratios have declined from about 75% to about 35%. Although we do not consider this latter value particularly low for management purposes, the rate of decline should be of concern.

The relation of stock to subsequent recruits showed a distinct temporal trend (Fig. 8), although this should be viewed with some skepticism. Recruitment to

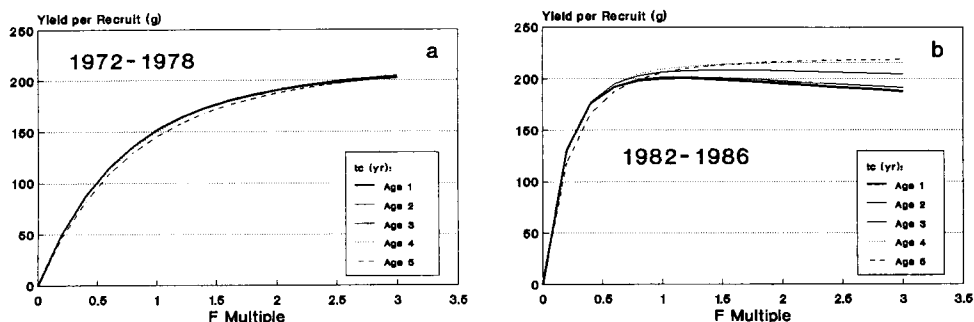


Figure 10. Overall yield per recruit of red porgy at an intermediate level of natural mortality ($M = 0.28$) under (a) 1972–1978 conditions (population F for ages 1–9 equals 1.0/yr, F -multiple equals 1.0, and age at entry of 1); and (b) 1982–1986 conditions (population F for ages 1–9 equals 3.7/yr, F -multiple equals 1.0, and age at entry of 1).

age-1 started high in 1972 and declined, first with increasing spawning stock biomass to 1976–1979, and then with decreasing spawning stock biomass through 1986. The relatively low inter-annual variability in recruitment could suggest that a density-dependent factor was most important, rather than multiple observations of a single habitat-determined level of recruitment plus random error. Ehrlich (1975) and others champion habitat limits although these may be more important to species more obviously territorial than red porgy. Although red porgies on the Carolina continental shelf may not produce all, or a major portion, of recruits to their population, predation, cannibalism and competition for food and space could produce density-dependent control of recruitment. Since the duration of the trend is less than a full cycle and most time series techniques require at least three full cycles, it is not possible to ascribe the cause for the decline in recruitment to either stock-dependency or some environmental factor.

Because red porgy undergo a sex change from female to male as they age, spawning stock ratios which include the male portion of the mature stock tend to be lower than those based solely on the female biomass (Fig. 9). The equilibrium estimates of SSR are based on the fishing year estimates on fishing mortality rates and therefore reflect the expected lifetime reproductive potential (expressed as biomass) of an individual recruit given the age-specific estimates of fishing mortality (Fig. 9a). The nonequilibrium estimates of SSR are based on the cohort estimates of fishing mortality rates and therefore represent the realized lifetime reproductive potential (again, expressed as biomass) of an individual recruited to that cohort (Fig. 9b). Clearly SSR was high during the 1970s when fishing mortality rates were low (70% to 80%), and have dropped significantly to 30% to 40% during the more recent period (1982–1986). Note that the estimated fishing mortality rates for a given year class (cohort) include estimated fishing mortality rates from as much as 9 or 10 years after the start of the cohort.

An analysis of yield per recruit shows that only a small increase in yield can be obtained by raising the age at which the red porgy are caught (Fig. 10). For the period 1972–1978 significant gains in yield would have been available by increasing F for all ages. During the period 1982–1986, these gains in yield were obtained and exceeded. The greater increase in F for younger red porgy (ages 1–4) compared to older red porgy (ages 5–9) is primarily due to the declining availability of the older fish with increased selection for the younger fish, and raises the possibility that maintaining yield per recruit at the levels available during the high exploitation period may require raising the age at entry.

The conclusion that little can be gained from increasing the age at entry (minimum size limits) arises from the use of age-specific fishing mortality in estimating yield per recruit, and differs from the conclusion of Huntsman et al. (1983), based on the assumption of constant-aged fishing mortality with knife-edged recruitment to the fishery. Since small fishing mortality is associated with these younger ages, especially for the low exploitation period, little gain to the stock could be obtained by foregoing these catches. However, as the trend towards increasing fishing mortality on younger ages continues (as seen in the relative increase in F for ages 1–4 versus 5–9), then potential benefits arise from increasing or maintaining yield per recruit by increasing age at entry (minimum size limits).

In summary, management is concerned both with growth overfishing and with recruitment overfishing. Only trivial gains in yield-per-recruit are obtainable through minimum size limits based on the analysis on the 1982–1986 period. However, with the apparent declines in spawning stock biomass between 1978 and 1982 and the relatively greater increase in the contribution of younger fish to the landings, overall fishing mortality needs to be controlled such that landings do not exceed 400,000 kg excessively, that is, landings such as the 755,000 kg obtained in 1982 should be avoided.

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